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A Comparison of Aquatic Macrophyte Communities in Regulated and Non-regulated Lakes, Voyageurs National Park and Boundary Waters Canoe Area, Minnesota

United States Department of the Interior

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Midwest Region

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A COMPARISON OF AQUATIC MACROPHYTE COMMUNITIES IN REGULATED AND NON-REGULATED LAKES, VOYAGEURS NATIONAL PARK AND BOUNDARY WATERS CANOE AREA, MINNESOTA

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ABSTRACT

The effects of water-level regulation on aquatic macrophyte communities, individual plant species, and potential faunal habitat were investigated in a study of two regulated lakes and an unregulated lake in northern Minnesota. Water levels in Rainy Lake and Namakan Reservoir in Voyageurs National Park are regulated by dams. Natural annual fluctuations of 1.8 m are replaced with fluctuations of 1.1 m in Rainy Lake and 2.7 m in the five lakes that comprise Namakan Reservoir. In addition, springtime peaking of water levels in Namakan Reservoir is delayed by one month. After reaching the peak, water levels in the regulated lakes are held at that level through the summer and allowed to gradually decline through autumn and winter. This study was conducted by estimating the cover of each plant species in randomly placed quadrats along transects that followed depth contours in the lakes. These contours were selected to represent different plant habitats, as defined by the timing and duration of flooding and dewatering in unregulated Lac La Croix.

Detrended correspondence analysis showed that the macrophyte communities at all depths of the regulated lakes differed from those in the unregulated lake. The differences were more profound in deeper parts of the littoral zone. Lac La Croix contained taxonomically and structurally diverse plant communities at all depths, maximizing faunal habitat. The greatest effect of regulation on Rainy Lake was along transects at the depth that is never dewatered. There were only four taxa present; they were all erect aquatics that extended through the entire water column and offered little structurally diverse faunal habitat. The greatest effect of regulation on Namakan Lake was along transects at the depth where drawdown occurs in early winter and disturbance results from ice formation in the sediments. Rosette and mat-forming species were dominant, providing minimal faunal habitat.

The hydrologic regime at Lac La Croix results in intermediate disturbance that maintains high diversity. There is too little disturbance from water-level fluctuations in Rainy Lake and too much disturbance in Namakan Reservoir, resulting in reduced diversity in both cases. The macrophyte communities of the regulated lake systems would benefit from a return to more natural hydrologic regimes. Namakan Reservoir should be regulated to reach its peak water level at the beginning of June, summer drawdowns should occur at both Rainy Lake and Namakan Reservoir, and the amplitude of annual drawdowns should vary between years but approximate 1.8 m. These hydrologic conditions should, over time, result in more diverse macrophyte communities and more diverse faunal habitat throughout the littoral zone of the regulated lakes.

TABLE OF CONTENTS

Page

ABSTRACT.....iii

LIST OF FIGURES.....v

LIST OF TABLES.....v

INTRODUCTION.....1

STUDY AREA.....2

METHODS.....5

RESULTS AND DISCUSSION.....7

Floristics.....7

Species Similarities Among Lakes.....10

Comparison of Lakes by Transect.....11

Structure of Aquatic Vegetation.....16

Influence of Aquatic Vegetation on Aquatic Fauna.....18

Physical and Biotic Interactions.....18

Invertebrates.....19

Muskrats.....22

Avifauna.....23

Fish.....24

CONCLUSIONS.....28

ACKNOWLEDGMENTS.....30

LITERATURE CITED.....30

APPENDIX.....38

LIST OF FIGURES

Figure — Page

1. Map of study area in northern Minnesota, showing the boundary of Voyageurs National Park, the major lakes, dam sites, and study sites.....3

2. Water-level regimes for Lac La Croix, Rainy Lake, and Namakan Reservoir, showing bounds of variation, computed natural water levels, and altitudes of study transects (adapted from Flug 1986).....4

3. Two-dimensional plot of DCA ordination of the Importance Value X transect matrix (Eigenvalues: Axis 1 = 0.879, Axis 2 = 0.403). Points plotted are transects, labeled by lake, site, and transect codes.....12

4. Two-dimensional plot of DCA ordination of the Importance Value X transect matrix (Eigenvalues: Axis 1 = 0.879, Axis 2 = 0.403). Points plotted are selected taxa.....13

5. Diagrammatic cross-sections of the littoral zone of study sites in Lac La Croix, Rainy Lake, and Namakan Lake. The general structural groups of the 30 most important taxa, as might be viewed by aquatic fauna, are depicted at the water depths sampled along transects **b**, **c**, and **d**.....20

LIST OF TABLES

Table — Page

1. Importance Values (IV) of plant taxa found on transects **a-d** at sites 1 and 2 at Lac La Croix, Rainy Lake, and Namakan Lake.....8

2. Mean Importance Values (IV) of the 30 most prominent taxa on transects **b**, **c**, and **d** of Lac La Croix, Rainy Lake, and Namakan Lake. Taxa are separated into morphologically similar groups.....17

3. Predicted fish use of macrophytes as spawning, nursery, and adult feeding habitat along transects **b**, **c**, and **d** in Lac La Croix, Rainy Lake, and Namakan Reservoir (refer to Figure 5).....27

INTRODUCTION

Several dams regulate the water levels in a chain of large lakes along the Rainy River in Voyageurs National Park. Water levels in the upstream lakes, collectively called Namakan Reservoir, are regulated by two dams on the outlet of Namakan Lake. Water levels in Rainy Lake are controlled by a dam on its outlet and also by regulation of the upstream lakes. As a result of the regulation, natural annual fluctuations of about 1.8 m have been replaced by fluctuations of about 1.1 m on Rainy Lake and 2.7 m on the upstream lakes (Flug 1986). In addition, the timing of water-level change is altered in both systems. The altered hydrologic conditions likely interact to create different environments or habitats for the various biotic components of the ecosystem. Although the enabling legislation for the park directed the National Park Service (NPS) to work within the established water regulatory system in managing park resources, it is National Park Service policy to manage resources in their natural state. Therefore, a comprehensive research effort was initiated to investigate the effects of the current regulatory system and evaluate alternatives.

Hydrologic studies have been completed that model the water-level fluctuations and provide simulation capabilities (Flug 1986). Other studies (Kallemeyn et al. 1988) have shown the effects of these fluctuations on fish (Kallemeyn 1987a, 1987b, 1989), birds (Reiser 1988, Cuthbert and Rothstein 1988), mammals (Route and Peterson 1988, Smith and Peterson 1988, Thurber and Peterson 1988), benthic invertebrates (Kraft 1988), and primary productivity and water chemistry (Kepner and Stottlemyer 1988).

A study was also conducted to investigate the differences in plant communities resulting from water-level regulation (Monson 1986). However, significant differences were not found between lakes with different water-level regimes, primarily because of problems with the sampling design and too few sampling plots to obtain statistically valid data. Vegetation assessments performed as part of a waterfowl study (Reiser 1988) suggested that significant differences do exist (H. Reiser, pers. comm.). These differences would be an expected result of the development of different habitats in the altered systems.

As a result of altered hydrology in the regulated lakes, some aquatic and wetland plant habitats are flooded during parts of the growing season when drawdown conditions would normally occur, and other habitats experience springtime drawdown when none would occur naturally. The length of time that the habitats are exposed to non-natural water-level conditions is also altered. Thus, plant species that can tolerate both spring drawdown and flooding for long periods of time should be favored in Rainy Lake and Namakan Reservoir. A more structurally diverse community would be expected in a non-regulated lake because plants are subject to greater natural habitat variation and cannot become firmly established in areas where their ideal environments are maintained by regulation. Aquatic macrophyte communities are known to respond to water-level differences over time in both regulated (Nichols 1975) and natural

systems (van der Valk 1981), and responses to periodic flooding are well-documented in many plant species (Kozlowski 1984). Zonation of aquatic plants along depth gradients is well-known (Sculthorpe 1967, Spence 1982), but zonation or any other aspect of vegetation related to altered hydrologic patterns is less studied, particularly in larger lakes (Keddy and Reznicek 1986).

In this study, we focused on Rainy Lake (where water-level fluctuations have been reduced below natural conditions), Namakan Lake (where they have been increased above natural conditions), and on Lac La Croix, a non-regulated lake in the Boundary Waters Canoe Area that served as a control.

The study was undertaken to address the following questions:

1. What changes in the littoral zone communities have resulted from alterations of annual water-level fluctuations in Namakan and Rainy lakes?

2. Which, if any, aquatic macrophyte species have been impacted most heavily?

3. What is the significance of any macrophyte alteration in terms of changes in habitat and food availability for waterfowl, fish, and aquatic mammal populations?

STUDY AREA

Voyageurs National Park is situated on the United States-Canadian border in the state of Minnesota (Figure 1). There are 30 lakes in the park, totaling approximately 34,400 hectares of surface area. Four of the lakes contribute 96 percent of the total lake surface area in the park. The largest of the lakes is Rainy Lake, which has a total surface area of 89,357 ha, with approximately 14,600 ha in the park. The water-level control structure is a hydroelectric dam that was constructed in 1909 across the outlet at International Falls, Minnesota and Fort Francis, Ontario. Namakan Reservoir consists of Namakan, Kabetogama, Sand Point, Crane, and Little Vermilion lakes; the first three are at least partially within the park and have a within-park surface area of 18,410 ha. Water levels were originally controlled by natural rock sills at the outlet of Namakan Lake at Kettle Falls. Two dams were contructed at this outlet in 1914, and they are now used to regulate water levels.

The dams and lake levels are regulated by the International Joint Commission because the lakes cross the U.S.-Canadian border. The water management program sets acceptable high and low limits (termed "rule curves") for water levels throughout the year (Figure 2). Although the mean annual fluctuations of water levels under natural conditions would be 1.9 m for Rainy Lake and 1.8 m for Namakan Lake, regulation results in mean annual fluctuations of 1.1 m and 2.7 m, respectively (Flug 1986). However, the rule curves allow for annual fluctuations as low as 0.6 m on Rainy Lake and as

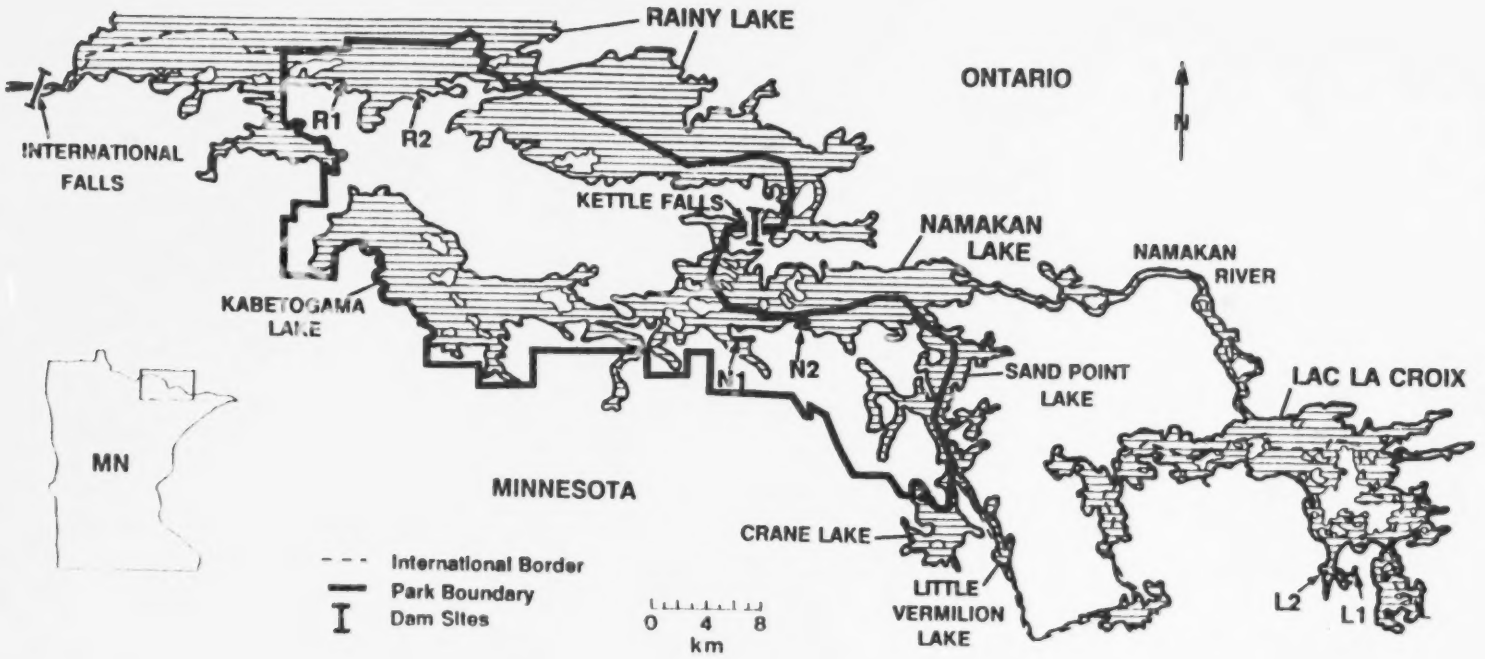

Figure 1. Map of study area in northern Minnesota, showing the boundary of Voyageurs National Park, the major lakes, dam sites, and study sites.

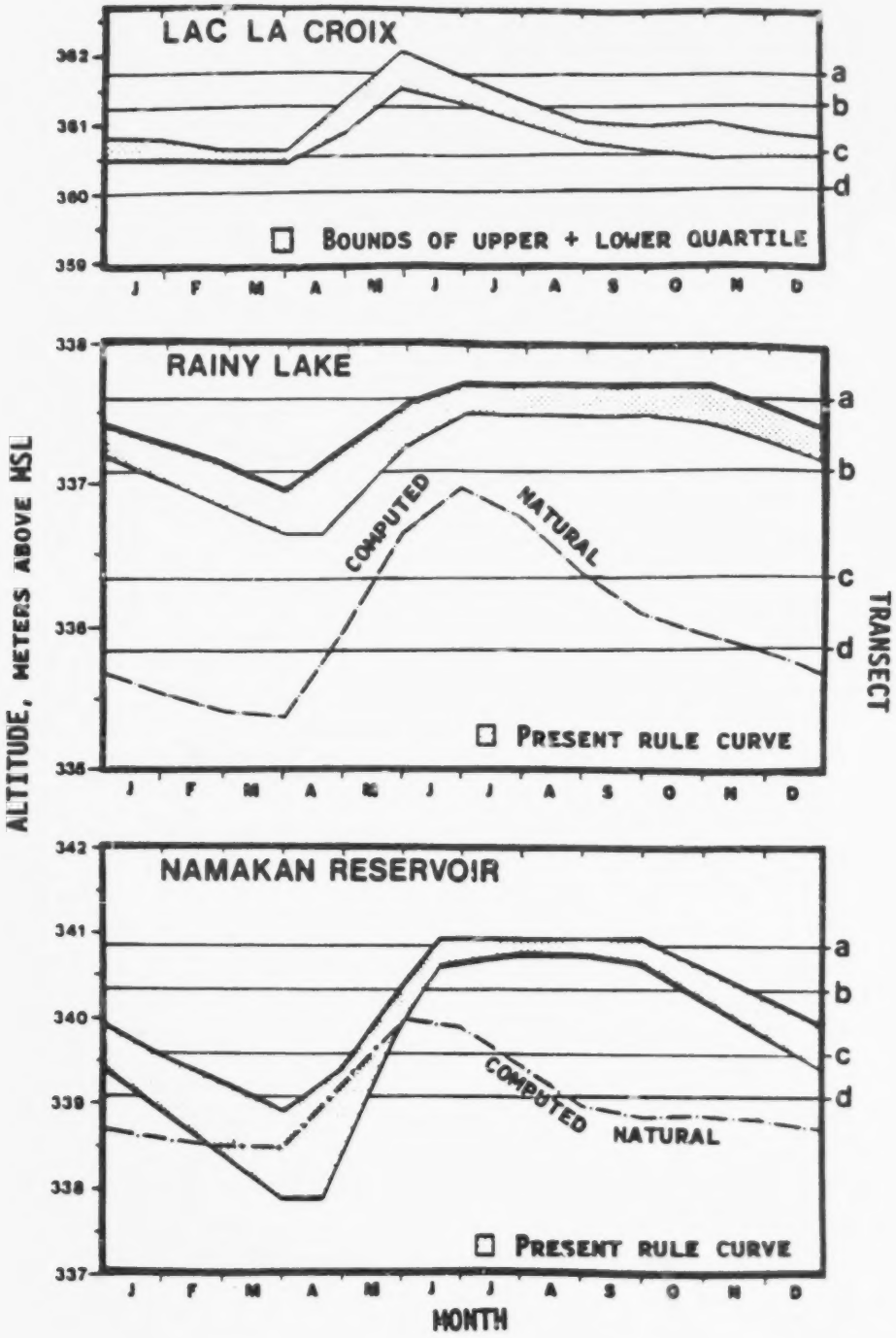

Figure 2. Water-level regimes for Lac La Croix, Rainy Lake, and Namakan Reservoir, showing bounds of variation, computed natural water levels, and altitudes of study transects (adapted from Flug 1986).

high as 3.0 m on Namakan Reservoir. The lakes are regulated to reach peak levels in late June or early July, rather than immediately following spring runoff as much as a month earlier. The water levels are then held stable throughout the summer and allowed to decline gradually through autumn and winter, as opposed to a gradual decline that would naturally begin just following the peak.

Lac La Croix is a natural lake upriver from Rainy Lake and Namakan Reservoir that is similar to those lakes in most aspects; however, its water levels are not regulated. The mean annual fluctuation of water levels is approximately 1.6 m (Figure 2). The peak occurs in late May or early June, and water levels then decline gradually until spring runoff occurs the following April. In addition, the degree of variability in annual water-level regimes is different from that of the regulated lakes because the rule curves reduce the variability in Rainy Lake and Namakan Reservoir. Although both Rainy and Namakan lakes deviate from the guidelines as much as 19% of the time, the annual variation is more extreme at Lac La Croix, ranging from 0.3 m to 3.0 m. The study lakes all have medium water clarity and moderate alkalinity (Kepner and Stottlemyer 1938, Minnesota Department of Natural Resources, unpublished data).

Two study sites each were selected at Rainy Lake, Namakan Lake, and Lac La Croix (Figure 1) following a reconnaissance flight in a small aircraft and follow-up inspections by boat. Much of the shoreline in these lakes consists of steeply sloping granitic bedrock, so site selections were heavily dependent on geology and basin morphology. Sites with similar basin size, geometry, and orientation were chosen to reduce variability due to disturbance from wind and waves. Since sampling was planned at certain altitudes (water depths), each site was also required to have a minimum depth. All sites had veneers of loosely consolidated, mixed organic sediment above a fine-grained, consolidated clay substrate. Each site had some anomalous areas, most often small pockets of rocky or gravelly substrate. This situation could not be avoided, but these characteristics were encountered with similar frequency at each site. The selected sites at Rainy Lake were just east of Dove Bay (R1) and at Alder Creek (R2). The sites at Namakan Lake were at Sheen Point (N1) and Deep Slu (N2). At Lac La Croix, the sites were at the east (L1) and west (L2) sides of Lady Boot Bay (Figure 1).

METHODS

Four transects were sampled at each study site in 1987 (see Figure 2). The transects were established nearly parallel to the shoreline at altitudes relative to mean annual high water (MHW). The altitudes (described as depth from MHW) were selected to represent specific habitat types in the non-regulated control lake, Lac La Croix. By also sampling at these altitudes on the regulated lakes, the effects of altered hydrologic regimes on plant communities could be shown. The four transects at each site were labeled **a-d**, resulting in site-transect designations such as R1a, N2b, N2c, and L1d. The altitudes of the transects and the

respective habitats in Lac La Croix (along with comparisons for the other lakes) were:

a. 0.0 m - Shoreline. This zone is minimally flooded at the peak water level in late May-early June but is soon dewatered and remains so throughout the growing season. Moist soil species that cannot tolerate prolonged inundation should be dominant. In Rainy and Namakan lakes, this zone is usually flooded in June and remains minimally flooded throughout the growing season, as drawdown does not occur until early-mid autumn. In some years, water levels in these lakes are in the lower range of the rule curve, and dewatered conditions similar to Lac La Croix exist.

b. 0.5 m - Amphibious. This zone is flooded in May, remains so during the early part of the growing season, and then is dewatered in mid-July. It should contain plants, such as emergents, that are capable of existing in both aquatic and terrestrial habitats. In Rainy and Namakan lakes, this zone is flooded in May or June, remains at this water depth throughout the growing season, and then undergoes gradual drawdown, becoming dry in November in Namakan Lake and in February in Rainy Lake.

c. 1.25 m - Submersed. This zone is flooded in April and remains so throughout the growing season; it is often dewatered again in February. It should contain aquatic species that can tolerate late winter drawdown and perhaps some deep water emergents. This zone is always submersed in Rainy Lake; it is dry in spring and flooded in May in Namakan Lake. In both of these lakes, the zone remains at a 1.25 m depth throughout the growing season and then undergoes gradual drawdown.

d. 1.75 m - Deep water. This zone is inundated throughout almost all years. It should contain aquatic species capable of tolerating deep water and may be at the limit of plant growth. This zone is always submersed in Rainy Lake; it is dry in early spring and then flooded in April or May in Namakan Lake. In both of these lakes, this zone remains at a 1.75 m depth throughout the growing season and then undergoes gradual drawdown.

Water levels vary considerably from year to year in all three study lakes, and they were low in 1987. However, since the established plant communities were more likely to correspond to the long-term, normal hydrologic regime, all transects were established at altitudes relative to MHW, not to the water levels of 1987. Actual water levels in 1987 at the time of sampling were 0.5 m below MHW in Lac La Croix, 0.8 m below MHW in Rainy Lake, and 0.1 m below MHW in Namakan Lake. The only transects exposed to water-regime conditions that would not typically occur during the growing season were the 0.5-m transects (b) at Rainy Lake, which were dewatered instead of flooded.

Twenty 1 x 1 m sampling quadrats were randomly located on each of the four transects at each of the six sites. At each quadrat, species identifications and percent cover estimations were made. In water too deep to wade, sampling was conducted from a canoe using a diving mask to aid underwater vision. Taxa present in very small amounts (less than 1 percent cover) were systematically recorded as 0.5%. Since plants may occupy space at different strata, cover estimates for each quadrat could exceed 100%. Plant names used conform to the nomenclature of Voss (1972, 1985) whenever possible. Those taxa not included in Part I or II of Michigan Flora are named according to Gleason and Cronquist (1963).

The vegetation data were summarized by lake and by transect, using summary statistics, Sorenson's index, and ordination. Importance Values (IV) were calculated as the sum of relative frequency and relative mean cover of each taxa on each transect. The IV vs. transect matrix was analyzed by detrended correspondence analysis (DCA, McCune 1987) to give ordinations of both transects and species. Since the purpose of the ordination was to assess general community patterns, rather than rare species occurrences, the total number of taxa used in the ordination was reduced from 109 to 71 by dropping those taxa found in less than one percent of the total number of quadrats.

RESULTS AND DISCUSSION

Floristics

A total of 109 taxa were sampled across all transects at all lakes (Table 1). Rainy Lake had a slightly greater species richness (76 taxa) than either Namakan Lake (72) or Lac La Croix (65). This is not surprising since species richness often increases after many years of water-level regulation (Nichols 1975), but the taxa present may not all be natural components of the system. Of the 109 total taxa sampled, 20 were unique to Rainy Lake, 12 to Namakan Lake, and 11 to Lac La Croix. Many of the taxa unique to Rainy Lake could have responded to the unusually low water levels that occurred in early-mid summer, 1987. These taxa include a number of species in the sedge family (Cyperaceae), such as Carex sychnocephala, Carex crawfordii, Cyperus aristatus, Cyperus strigosus, Fimbristylis autumnalis, and Hemicarpha micrantha (common names for all plant taxa are provided in the Appendix).

Table 1. Importance Values of plant taxa found on transects a-d at sites 1 and 2 at Lac La Croix, Rainy Lake, and Namakan Lake. Asterisk denotes presence of taxa that were not included in DCA ordination and for which no Importance Value was calculated.

Species	L1				L2				R1				R2				M1				M2			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Acer rubrum L.	-	-	-	-	*	-	-	-	*	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Acorus calamus L.	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	*	-	-	-	*	-	-	-
Agrostis hyemalis (Walter) BSP.	1.7	-	-	-	0.4	-	-	-	1.6	1.2	-	-	2.6	2.9	-	-	2.0	-	-	-	-	-	-	-
Alnus spp.	*	-	-	-	*	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-
Anemone canadensis L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Aster spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Betula spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Bidens beckii Torr.	-	0.5	3.0	1.2	-	5.6	20.8	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-	-
Bidens cernua L.	-	-	-	-	-	-	-	-	1.1	-	-	-	1.4	7.2	-	-	-	-	-	-	-	-	-	-
Calamagrostis canadensis (Michaux) Beauv.	11.0	-	-	-	21.5	-	-	-	17.4	-	-	-	16.6	-	-	-	19.9	-	-	-	25.1	-	-	-
Campanula aparinoides Pursh.	0.8	-	-	-	2.2	-	-	-	0.4	-	-	-	-	-	-	-	1.6	-	-	-	2.6	-	-	-
Cardamine pensylvanica Willd.	-	-	-	-	0.4	-	-	-	-	-	-	-	0.7	-	-	-	0.4	1.4	0.4	-	-	-	-	-
Carex crawfordii Fern.	-	-	-	-	-	-	-	-	5.2	4.4	-	-	-	3.6	-	-	-	-	-	-	-	-	-	-
Carex hirta L.	-	-	-	-	-	-	-	-	4.0	3.3	-	-	-	5.3	-	-	-	-	-	-	-	-	-	-
Carex lacustris Willd.	22.5	-	-	-	15.5	-	-	-	0.4	-	-	-	1.9	0.3	-	-	16.5	6.6	-	-	2.3	-	-	-
Carex rostrata Stokes	0.5	-	-	-	1.9	-	-	-	6.0	0.8	-	-	9.1	-	-	-	9.5	16.2	-	-	20.1	10.8	-	-
Carex stricta Lam.	*	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex sychnocephala Carey	-	-	-	-	-	-	-	-	0.8	-	-	-	-	5.8	-	-	-	-	-	-	-	-	-	-
Carex vesicaria L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Carex viridula Michaux	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chara spp.	-	-	11.9	16.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	34.4	-	-	4.2	22.8
Cicuta bulbifera L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.9	-	-	-	0.7	-	-	-
Cirsium sp.	-	-	-	-	-	-	-	-	-	-	-	-	*	*	-	-	-	-	-	-	-	-	-	-
Cyperus aristatus Rottb.	-	-	-	-	-	-	-	-	0.8	3.5	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-
Cyperus strigosus L.	-	-	-	-	-	-	-	-	1.7	4.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elatine minima (Nutt.) Fischer & C. Meyer	-	0.5	-	-	-	7.8	-	-	-	-	-	-	-	-	-	-	-	3.8	-	0.5	-	9.9	7.0	8.3
Eleocharis acicularis (L.) R. & S.	-	15.9	-	-	0.4	26.7	-	-	0.9	6.4	10.9	-	1.3	4.5	3.5	-	0.4	6.2	33.4	7.9	-	6.9	9.4	6.2
Eleocharis obtusa (Willd.) Schultes	-	-	-	-	-	-	-	-	2.4	15.2	-	-	-	1.9	-	-	-	-	-	-	-	-	-	-
Eleocharis smallii Britton	2.6	11.9	-	-	-	3.7	-	-	1.0	1.0	5.8	-	1.9	0.3	-	-	0.4	-	-	-	0.7	2.8	-	-
Epilobium coloratum Biehler	-	-	-	-	-	-	-	-	0.8	0.9	-	-	1.1	1.2	-	-	-	-	-	-	0.7	-	-	-
Equisetum arvense L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-
Equisetum fluviatile L.	-	*	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fimbristylis autumnalis (L.) R. & S.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Fragaria virginiana Miller	-	-	-	-	*	-	-	-	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fraxinus spp.	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Galium trifidum L.	3.1	-	-	-	4.3	-	-	-	1.8	-	-	-	0.8	-	-	-	-	-	-	-	1.4	-	-	-
Geranium bicknellii Britton	-	-	-	-	-	-	-	-	0.8	3.0	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-
Gerardia tenuifolia Vahl.	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glyceria borealis (Nash) Batch.	-	15.9	-	-	-	10.7	-	-	0.4	1.5	-	-	-	1.5	-	-	-	5.4	13.8	-	2.7	13.1	0.9	-
Glyceria canadensis (Michaux) Trin.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-
Glyceria grandis S. Watson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-
Hemicarpha micrantha (Vahl.) Pax	-	-	-	-	-	-	-	-	-	*	-	-	-	*	-	-	-	-	-	-	-	-	-	-
Hypericum majus (A. Gray) Britton	5.0	-	-	-	5.0	-	-	-	8.6	12.2	-	-	5.8	13.1	-	-	0.4	3.1	-	-	-	0.5	-	-
Impatiens capensis Meerb.	-	-	-	-	-	-	-	-	0.4	-	-	-	-	-	-	-	2.2	-	-	-	0.7	-	-	-
Isoetes echinospora Durieu.	-	-	-	-	-	2.3	-	-	-	-	21.1	-	-	-	16.5	-	-	3.1	7.5	5.8	-	5.3	2.5	8.6
Juncus brevicaudatus (Engelm.) Fern.	4.3	5.0	-	-	4.0	-	-	-	0.4	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus effusus L.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus pelocarpus Meyer	0.4	-	-	-	-	-	-	-	2.1	8.1	-	-	0.4	0.9	-	-	-	-	-	-	-	-	-	-
Lathyrus palustris L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Lemna spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	*	-	-	-
																					-	6.4	-	-

Table 1. (continued)

Species	L1				L2				R1				R2				M1				M2			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Lycopus americanus Muhl.	-	-	-	-	-	-	-	-	0.4	-	-	-	0.5	-	-	-	5.6	-	-	-	3.1	-	-	-
Lysimachia terrestris (L.) BSP.	5.4	-	-	-	5.5	-	-	-	2.7	-	-	-	4.8	-	-	-	5.1	-	-	-	12.5	-	-	-
Lysimachia thyrsiflora L.	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mentha arvensis L.	1.8	-	-	-	4.8	-	-	-	-	-	-	-	0.7	-	-	-	-	-	-	-	2.8	-	-	-
Myrica gale L.	3.4	-	-	-	1.4	-	-	-	6.2	-	-	-	1.3	-	-	-	3.5	-	-	-	2.2	-	-	-
Myriophyllum spp.	-	1.4	7.1	2.6	-	1.1	26.1	25.4	-	-	-	-	-	-	1.4	-	-	-	-	2.2	-	-	-	1.1
Najas flexilis (Willd.) Rostik. & Schmidt	-	7.1	41.0	29.9	-	4.0	2.2	-	-	-	-	-	-	-	8.0	-	-	1.5	3.3	5.6	-	-	0.9	4.3
Nitella sp.	-	-	-	-	-	-	4.4	15.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nuphar variegata Durand	-	1.1	2.3	-	-	-	-	-	-	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nymphaea odorata Aiton	-	1.5	14.8	-	-	9.9	24.2	13.2	-	-	-	-	-	-	-	-	-	-	5.4	4.6	-	-	-	1.1
Onoclea sensibilis L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-
Oxalis fontana Bunge	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Panicum sp.	-	-	-	-	-	-	-	-	0.4	3.1	-	-	1.7	1.8	-	-	-	-	-	-	-	-	-	-
Poa pratensis L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Polygonum amphibium L.	4.2	-	-	-	1.5	-	-	-	1.2	0.9	-	-	5.1	-	-	-	1.9	-	-	-	2.7	2.1	-	-
Polygonum lapathifolium L.	-	-	-	-	-	-	-	-	7.3	18.1	-	-	7.1	31.0	-	-	0.4	25.4	6.9	-	-	6.4	3.8	-
Polygonum punctatum Ell.	-	-	-	-	-	3.2	-	-	2.0	3.5	-	-	8.0	3.9	-	-	1.3	-	-	-	5.0	1.6	-	-
Polygonum sagittatum L.	-	-	-	-	-	-	-	-	3.6	0.6	-	-	1.1	0.6	-	-	0.5	-	-	-	-	-	-	-
Populus spp.	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-	-	-	-	-	+	-	-	-
Potamogeton amplifolius Tuckerman	-	-	-	-	-	-	-	26.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potamogeton epihydrus Raf.	-	4.8	0.7	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Potamogeton foliosus Raf.	-	-	1.0	7.7	-	-	-	-	-	-	1.7	-	-	-	7.5	4.6	-	-	-	8.8	-	-	-	-
Potamogeton gramineus L.	-	3.7	-	-	-	2.8	-	-	-	-	5.4	-	-	-	3.1	6.0	-	0.5	2.4	0.5	-	-	2.4	3.0
Potamogeton richardsonii (Benn.) Rydb.	-	-	2.8	3.1	-	0.5	5.1	2.7	-	-	1.2	22.4	-	-	6.7	9.6	-	1.0	0.9	7.6	-	-	-	13.7
Potamogeton robbinsii Oakes	-	-	1.0	19.4	-	-	-	-	-	-	-	-	-	-	8.6	-	-	-	-	-	-	-	-	-
Potamogeton spirillus Tuckerman	-	8.4	7.0	4.9	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	1.4	-	-	-	0.5	2.7
Potamogeton vaseyi Robbins	-	-	2.1	-	-	2.2	-	-	-	-	-	-	-	-	-	-	-	-	2.1	9.5	-	-	-	-
Potamogeton zosteriformis Fern.	-	-	2.1	0.7	-	-	3.3	6.3	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	0.4
Potentilla norvegica L.	-	-	-	-	-	-	-	-	4.4	1.2	-	-	7.3	7.2	-	-	0.5	-	-	-	-	-	-	-
Potentilla palustris (L.) Scop.	1.1	-	-	-	3.9	-	-	-	-	-	-	-	2.3	-	-	-	1.6	-	-	-	1.2	-	-	-
Ranunculus longirostris Godron	-	-	0.5	-	-	2.2	3.2	-	-	-	-	-	-	-	-	-	-	0.5	0.9	2.6	-	-	-	0.4
Ranunculus pennsylvanica L. T.	0.4	-	-	-	3.2	-	-	-	0.4	-	-	-	-	-	-	-	1.1	-	-	-	-	-	-	-
Ranunculus reptans L.	0.4	-	-	-	1.4	-	-	-	2.3	4.2	-	-	1.1	2.5	-	-	1.5	15.7	0.9	-	2.9	24.9	42.0	1.8
Rorippa palustris (L.) Besser	-	-	-	-	-	-	-	-	-	0.3	-	-	1.3	2.5	-	-	0.4	0.5	1.4	-	-	-	-	-
Rosa palustris Marsh.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sagittaria latifolia Willd.	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sagittaria rigida Michaux	-	+	-	-	-	+	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-
Sagittaria spp.	-	8.3	-	-	-	3.0	-	-	-	0.3	14.8	-	-	-	4.1	-	-	0.5	2.7	1.0	-	-	8.6	-
Scirpus cyperinus (L.) Kunth	3.1	-	-	-	0.6	-	-	-	4.4	-	-	-	11.1	-	-	-	6.4	-	-	-	4.5	-	-	-
Scutellaria galericulata L.	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-
Sium suave Walter	2.9	6.5	-	-	4.5	3.4	-	-	1.2	0.3	-	-	1.9	-	-	-	1.9	0.5	-	-	-	-	-	-
Solidago graminifolia (L.) Salisb.	7.8	-	-	-	2.9	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-
Sparganium chlorocarpum Rydb.	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sparganium eurycarpum Engelm.	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Sparganium fluctuans (Morong) Robinson	-	4.7	-	-	-	6.7	-	-	-	-	15.1	-	-	-	13.0	-	-	-	-	-	-	-	0.6	-
Spiraea alba Duroi	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Stachys palustris L.	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Subularia aquatica L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Thelypteris palustris Schott.	12.7	-	-	-	10.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-
Tillaea aquatica L.	-	-	-	-	-	-	-	-	1.1	0.6	-	-	-	1.0	-	-	0.4	8.5	12.6	8.4	-	9.4	11.9	6.5
Triadenum fraseri (Spach.) Gl.	4.2	-	-	-	1.9	-	-	-	0.8	-	-	-	0.	-	-	-	4.3	-	-	-	1.6	-	-	-
Typha latifolia L.	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Utricularia vulgaris L.	-	0.5	0.5	-	-	2.2	2.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vallisneria americana Michaux	-	-	2.1	11.7	-	-	8.0	10.8	-	-	24.0	77.6	-	-	26.9	9.8	-	-	5.1	-	-	-	5.3	19.0
Verbena hastata L.	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Veronica anagallis-aquatica L.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Viola spp.	0.4	-	-	-	1.2	-	-	-	0.4	-	-	-	-	-	-	-	2.2	-	-	-	0.7	-	-	-
Zizania palustris L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-

Species found only at the Namakan Lake sites included three shoreline grasses, Glyceria grandis, G. canadensis, and Poa pratensis, which apparently can exploit the drawdown that occurs in the lake each year (Nilsson and Keddy 1988). Species encountered only at Lac La Croix included emergents such as Carex stricta, Carex viridula, Equisetum fluviatile, and Juncus effusus. In addition, Sagittaria differentiated beyond the rosette stage and identifiable as S. latifolia was found only at Lac La Croix.

Northern wild rice, Zizania palustris, was conspicuously absent from the sampling in both Namakan Lake and Lac La Croix. In Lac La Croix, however, viable stands of wild rice were observed in wetlands adjacent to those sampled, and the species seems to be locally abundant elsewhere in the lake. Northern wild rice does not grow well in areas with wide water-level fluctuations (Nichols 1975) and is intolerant of both low water levels and flooding (Thomas and Stewart 1969, Pip and Stepaniuk 1988). Low water levels allow seeds to desiccate, and rising water levels force too much energy to be directed into shoot elongation. Wild rice is almost totally absent from Namakan Lake, except for a few individuals observed from year to year near river mouths (L. Kallemeyn, pers. comm.).

The unique species noted above did not dominate any of the transects in any lake. Some of the taxa that were dominant in Lac La Croix were rare or missing in the sampled flora of the other lakes, however. Thelypteris palustris was not found in sampling at Rainy Lake, and it was very rare in Namakan Lake. This fern requires a wet soil habitat (Swink and Wilhelm 1979), which does not occur at the shoreline of the regulated lakes that are typically flooded throughout the summer. Glyceria borealis is favored by drawdown (Nichols 1975), and it was not common at Rainy Lake, which has less drawdown than the other lakes. Bidens beckii was not found along any of the transects in Namakan Lake; Nymphaea odorata and the macroalgae Chara were not found in Rainy Lake. The observed distribution of these taxa may be an artifact of selected sampling sites, or it may relate to physical environment requirements or competitive interactions.

Species Similarities Among Lakes

In line with the objectives of this study, we deemed it important to determine some sense of the species pool available for colonization in each of the three lakes. If the available species were different among the three lakes, then any demonstrable differences in plant communities might not be attributable to the differences in water-level regimes. For this analysis, it was assumed that if an individual species was sited in a lake, it was likely that seeds or propagules of that species were available for future colonization.

Sorenson's index (Mueller-Dombois and Ellenberg 1974), computed using all species sampled in the lakes, showed the species pools to be similar. The similarity values were 61.0% between Rainy Lake

and Lac La Croix, 66.2% between Rainy Lake and Namakan Lake, and 70.1% between Lac La Croix and Namakan Lake. These values compare to similarities of 74% for sedge meadows in Wisconsin and Cook County, Illinois (Curtis 1959) and 52% for temporary pools in buttonbush swamps in Ohio (Tyrrell 1987). The greatest similarity was between Namakan Lake and Lac La Croix, the lakes with the greatest ranges of water-level fluctuation. Rainy and Namakan lakes were next most similar; they are both flooded throughout the growing season. In general, the three lakes share a high percentage of species; there-fore, it is reasonable that differences in communities at various depths are a result of different water-level regimes rather than different species pools. Some of the taxa that were not shared by the lakes could be selected against by the water-level regimes.

Comparison of Lakes by Transect

The aquatic plant communities in Lac La Croix, Rainy Lake, and Namakan Lake differed from each other, particularly at the greater depths sampled. In contrast, the two study sites at each lake were similar to each other; they seemed to adequately represent each lake. The DCA ordination (Figure 3) showed that the transects at any given water depth in an individual lake had very similar plant communities, as witnessed by the similarities in ordination coordinates (e.g., R1b and R2b). With the exception of the **c** and **d** transects of Lac La Croix, the plant communities within each lake were shown to differ with depth because the transect pairs plotted apart from each other (e.g., R1a-R2a, R1b-R2b, R1c-R2c, and R1d-R2d). These results are expected, since it is well-known that many plants have affinities and physiological adaptations for certain water-depth ranges (Sculthorpe 1967, Spence 1982, Kozlowski 1984, Wilcox and Simonin 1987, Hejny and Hroudova 1987). The plant communities at a given depth were shown to differ among the lakes, since these transect pairs plotted apart from each other (e.g., R1b-R2b, N1b-N2b, and L1b-L2b). These differences were less profound at the shoreline (**a** transects) than at greater depths (**c** and **d** transects). The ordination of vegetation data provides evidence that lakes with similar species pools but different hydrologic regimes develop different plant communities. Using different methods, similar conclusions were drawn by Nichols (1975) in the study of 20 sites in Wisconsin flowages and Rorslett (1989) in the study of 17 hydrolakes in Norway. In contrast to the conclusions of Monson (1986), the regulation of water levels on Rainy and Namakan lakes does alter the plant communities there.

In addition to the similarities and differences described above, the transect ordination scores suggest other, more subtle relationships between transects and lakes. Axis 1 scores are closely correlated with water depth ($r^2 = 0.85$, $p<0.0001$); shallow water transects have higher scores. Since the ordination scores for each transect are determined by the scores of species that dominate them, Figures 3 and 4 show shoreline transects and species to the right, amphibious transects and species in the middle, and aquatic transects and species to the left. The relationships

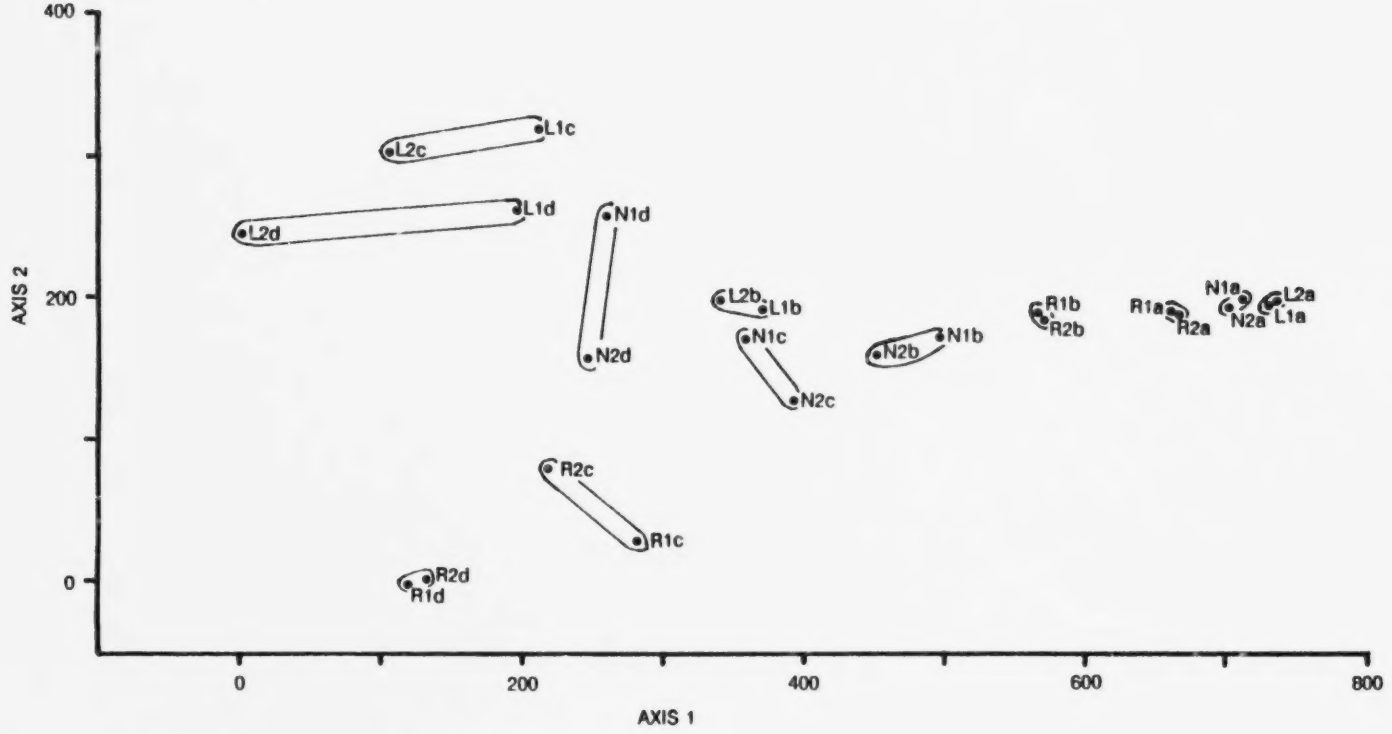

Figure 3. Two-dimensional plot of DCA ordination of the Importance Value X transect matrix (Eigenvalues: Axis 1 = 0.879, Axis 2 = 0.403). Points plotted are transects, labeled by lake, site, and transect code.

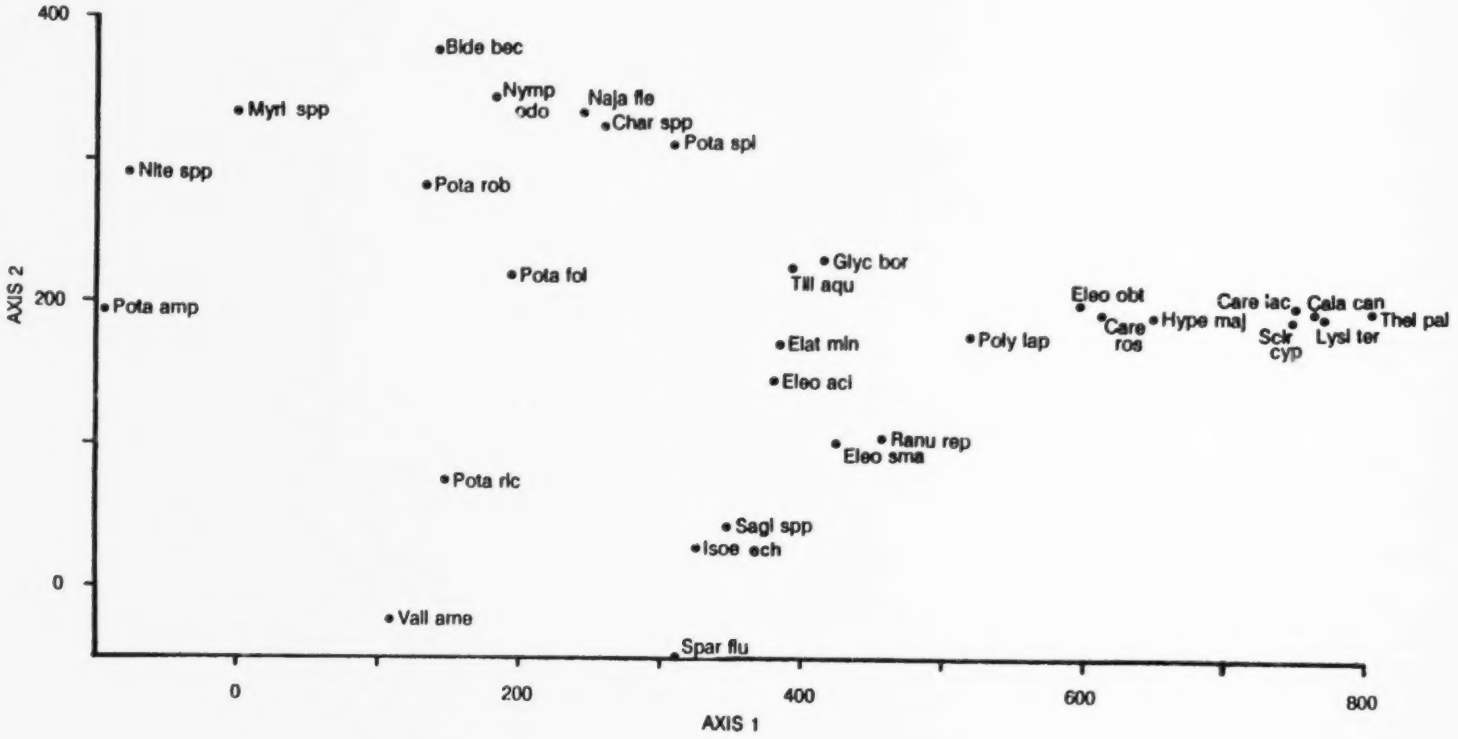

Figure 4. Two-dimensional plot of DCA ordination of the Importance Value X transect matrix (Eigenvalues: Axis 1 = 0.879, Axis 2 = 0.403). Points plotted are selected taxa.

between transects and species can be explored by analyzing the Importance Values presented in Table 1 and viewing the transect and species ordinations together.

Calamagrostis canadensis was a dominant species at the shoreline (transect **a**) of each lake. Carex lacustris and Thelypteris palustris were also dominant on the shoreline of Lac La Croix. Scirpus cyperinus, Carex rostrata, and Hypericum majus were also prevalent at Rainy Lake. Carex rostrata was also dominant on the shoreline of Namakan Lake, and Carex lacustris and Lysimachia terrestris were prevalent. Typically, these are all moist soil species, although Carex rostrata can also grow in shallow water (Voss 1972, 1985, Swink and Wilhelm 1979, Wilcox et al. 1985). Since all of these species have Axis 1 scores greater than 600 (Figure 4), all **a** transects cluster to the right in Figure 3. We used mean high water as the shoreline of the lakes in this study. As a result, transects R1a, R2a, N1a, and N2a do not have minimally flooded conditions throughout the growing season in all years. In low water years, these transects are ecologically similar to L1a and L2a; the similarities in vegetation between the shoreline transects reflect this fact.

On the 0.5-m transects (**b**), Lac La Croix was dominated by Eleocharis acicularis and Glyceria borealis, which are common in drawdown zones (Nichols 1975, Renman 1989, Rorslett 1989). Rainy Lake was dominated by Hypericum majus and Polygonum lapathifolium at this depth; the latter species is common on mudflats but may tolerate standing water (Swink and Wilhelm 1979, Voss 1985). The **b** transect of Namakan Lake was dominated by Polygonum lapathifolium, Carex rostrata, and mat-forming Ranunculus reptans. Differences in dominants at this depth caused differences in transect ordination scores. Transects R1b and R2b more closely resembled the shoreline transects (**a**) than did L1b, L2b, N1b, and N2b because Rainy Lake had lower-than-normal water levels in 1987 and more shoreline species growing along the dewatered 0.5 m transect.

On the 1.25 m transects (**c**), Lac La Croix was dominated by aquatic taxa Najas flexilis, Nymphaea odorata, Myriophyllum spp., and Bidens beckii; Rainy Lake was dominated by the aquatic Vallisneria americana and Sparganium fluctuans, plus Isoetes echinospora; Namakan Lake was dominated by Eleocharis acicularis, Ranunculus reptans, and Tillaea aquatica. The latter three species and Isoetes are low stature, bottom-dwelling plants favored by drawdown (Ashton and Bissell 1987, Renman 1989, Rorslett 1989). The lack of any similar dominants at this depth among lakes resulted in disparate transect ordination scores. Transects R1c and R2c have less similarity to their **b** transect counterparts than the **b** and **c** transects in Namakan Lake and Lac La Croix because there is a true habitat difference between the **b** and **c** transects in Rainy Lake; the **b** transects are amphibious and the **c** transects are always submersed. In Namakan Lake and Lac La Croix, these transects are both dewatered during parts of winter and spring.

On the 1.75 m transects (**d**), Lac La Croix had numerous prevalent aquatic taxa, including Vallisneria americana, Myriophyllum spp.,

Najas flexilis, Potamogeton amplifolius, Potamogeton robbinsii, and Chara spp. Only 4 species were encountered on the **d** transects at Rainy Lake; Vallisneria americana was the most dominant species, and Potamogeton richardsonii was also prevalent. Namakan Lake at this depth was dominated by Chara spp. and Potamogeton richardsonii and contained Vallisneria americana and bottom-dwelling Isoetes echinospora, Tillaea aquatica, and Eleocharis acicularis in substantial amounts. Again, the transect ordination scores differed widely between lakes. The paired ordination scores for Lac La Croix and Namakan Lake at this contour depth varied more than for other transect pairs because there were more species sharing the dominant role. Transect L2d is an outlier from the other transects because of the dominance of Potamogeton amplifolius and Nitella spp.

The ordination scores for Namakan Lake transects are compressed on both Axis 1 and Axis 2 (Figure 3). This is probably a result of drawdowns occurring on the deeper transects in Namakan Lake that limit the number of species that can grow well there. Potamogeton amplifolius, Nitella spp., Myriophyllum spp., Bidens beckii, and Potamogeton robbinsii were all absent from the **c** and **d** transects of the lake; they were dominant in Lac La Croix. Sparganium fluctuans was found only in small amounts on transect N2c; it was a dominant on the **c** transect of Rainy Lake that is never dewatered. The larger, erect aquatic macrophytes that did occur along the deeper transects in Namakan Lake seem to have survived by being deeply rooted in the mud cracks that were characteristic of the area. The deeper transects were dominated by mat-forming and low-growth aquatic species, plants whose morphology or physical structure can tolerate the extreme fluctuations in water levels. Eleocharis acicularis and Ranunculus reptans form vegetative mats that may competitively exclude other macrophytes through site preemption (Grace 1987); planting of Eleocharis acicularis is even under consideration as a mechanism for controlling undesirable aquatic plant growth (Ashton and Bissell 1987). Wilson and Keddy (1986) found that small rosettes and mat formers, which produced little shade and were usually not competitive dominants, could become dominant in environments where they could withstand damage that destroyed tall, leafy plants.

Ice is one damaging factor that may be important in drawdown zones. The **c** transect in Namakan Lake is under water when ice forms but then is dewatered in early winter, leaving blocks of ice resting on the bottom substrate. Near the upper part of the shore, the ice freezes solid with the bottom; in the lower part, frost grows into the water-saturated, silty bottom and causes upheaval through formation of needle ice (Renman 1989). Ranunculus reptans has a stoloniferous habit of growth that may make it sensitive to freezing and frost heave, but it aborts stolons and reduces mass prior to winter, thus increasing its ability to withstand frost heave (Renman 1989). The thin rhizomes of Eleocharis acicularis are broken into pieces by ice disturbance, but each piece of rhizome may grow vegetatively in the spring to become a new plant, helping this species to become dominant in this part of the dewatered zone (Renman 1989).

The **d** transects at Rainy Lake diverge from the other points plotted in Figure 3. The dense and leafy nature of Vallisneria americana and Potamogeton richardsonii extending through the water column probably shades out smaller, low-growth plant forms. Since dewatering never occurs at this depth to provide disturbance, no openings are created for invasion of other species.

Structure of Aquatic Vegetation

Aquatic macrophytes sometimes vary morphologically to adapt to different water-level conditions (Sculthorpe 1967). Examples of such plasticity include Potamogeton gramineus, Polygonum amphibium, and Ranunculus reptans, which have both aquatic and terrestrial forms (Sculthorpe 1967, Voss 1985). The physical structure or morphology of a plant must be suited to environmental conditions for the plant to survive. Therefore, it is possible that the plant communities in these lakes with different water-level regimes would differ in physical structure and thus provide different types of habitat for fish and wildlife.

We separated the 30 most important taxa (total IV) found in the study into six groups according to general structural characteristics, as might be viewed by aquatic fauna. These groups were: erect terrestrials, thin-stem emergents, mat formers, low rosettes, low growth aquatics, and erect aquatics. The Importance Values of the selected species were totalled by transect for each lake (Table 2). The erect terrestrial species were subsequently excluded from further discussion because they were similar among lakes and do not generally provide aquatic habitat. For similar reasons, the shoreline transects (**a**) were also excluded.

The shallow waters of Lac La Croix (0.5 m, transect **b**) support a structurally diverse plant community. Mat formers and low rosettes are present, providing plant cover at the lake bottom. Low growth aquatics extend this cover higher into the water column. Thin-stem emergents and erect aquatics extend through all or nearly all of the water column, with the erect aquatics providing more underwater surface area and cover than the thin-stem emergents (which also provide cover for wildlife above the water surface). In somewhat deeper waters in Lac La Croix (transects **c** and **d**), low growth and erect aquatics are all that are present, but they create a patchy environment with leaf surfaces for colonization and cover at all depths, plus areas of open water.

The shallow waters of Rainy Lake (transect **b**) differed from Lac La Croix in 1987 in that there are no low growth or erect aquatics present. This was expected because the transect was dewatered during that unusually dry season: thin-stem emergents, primarily Polygonum lapathifolium, replaced the aquatic species. Along the **c** transect, erect aquatics are present in numbers similar to Lac La Croix, but the lake bottom contains fewer low growth aquatics and, instead, has numerous low rosettes and some mat formers. These structure types offer less surface area and cover than do low growth aquatics. Along the **d** transect, erect aquatics are the only

Table 2. Mean Importance Values (IV) of the 30 most prominent plant taxa on transects b, c, and d of Lac La Croix, Rainy Lake, and Namakan Lake. Taxa are separated into morphologically similar groups.

Lake	La Croix			Rainy			Namakan		
Transect	b	c	d	b	c	d	b	c	d
Water depth (m)	0.5	1.25	1.75	0.5	1.25	1.75	0.5	1.25	1.75
Thin-stem emergents									
Carex lacustris	-	-	-	0.2	-	-	3.3	-	-
Carex rostrata	-	-	-	0.4	-	-	13.5	-	-
Eleocharis obtusa	-	-	-	3.6	-	-	-	-	-
Eleocharis smallii	7.8	-	-	0.7	2.9	-	1.4	-	-
Glyceria borealis	13.3	-	-	1.5	-	-	9.3	7.9	-
Polygonum lapathifolium	-	-	-	24.6	-	-	15.9	5.4	-
Scirpus cyperinus	-	-	-	-	-	-	-	-	-
Total:	21.1	0.0	0.0	36.0	2.9	0.0	43.4	13.3	0.0
Mat-formers									
Elatine minima	4.2	-	-	-	-	-	6.9	3.5	4.4
Eleocharis acicularis	21.2	-	-	5.5	7.2	-	6.5	21.6	7.1
Ranunculus reptans	-	-	-	3.4	-	-	20.2	21.3	0.9
Total:	25.4	0.0	0.0	8.9	7.2	0.0	33.6	46.4	12.4
Low rosettes									
Isoetes echinospora	1.2	-	-	-	18.8	-	4.2	5.1	7.2
Sagittaria spp.	5.6	-	-	0.2	9.5	-	0.3	5.6	0.5
Tillaea aquatica	-	-	-	0.8	-	-	9.0	12.1	5.9
Total:	6.8	0.0	0.0	1.0	28.3	0.0	13.5	22.8	13.6
Low-growth aquatics									
Chara spp.	-	6.0	8.1	-	-	-	-	2.3	28.5
Najas flexilis	5.5	21.6	14.9	-	4.0	-	0.8	2.1	5.0
Nitella spp.	-	2.2	7.8	-	-	-	-	-	-
Potamogeton robbinsii	-	0.5	9.7	-	4.3	-	-	-	-
Potamogeton spirilis	4.4	3.5	2.5	-	-	-	-	1.0	1.4
Total:	9.9	33.8	43.0	0.0	8.3	0.0	0.8	5.4	34.9
Erect aquatics									
Bidens beckii	3.1	11.9	0.6	-	0.4	-	-	-	-
Myriophyllum spp.	1.3	16.6	14.0	-	0.7	-	-	-	1.7
Nymphaea odorata	5.7	14.5	6.6	-	-	-	-	2.7	2.9
Potamogeton amplifolius	-	-	13.0	-	-	-	-	-	-
Potamogeton follosus	-	0.5	3.9	-	4.6	2.3	-	-	4.5
Potamogeton richardsonii	0.3	3.9	2.9	-	4.0	15.9	0.5	0.5	10.6
Sparganium fluctuans	5.7	-	-	-	14.0	-	-	0.3	-
Vallisneria americana	-	5.1	11.1	-	25.4	78.6	-	5.2	9.5
Total:	16.1	52.5	52.1	0.0	49.1	96.8	0.5	8.7	29.2
Grand total	79.3	86.3	95.1	45.9	95.8	96.8	91.8	96.6	90.1

structure type found in Rainy Lake. The patchiness, interspersed open-water areas, and dense cover at the lake bottom found in Lac La Croix are missing.

The shallow waters (transect b) of Namakan Lake differ from Lac La Croix in the same manner as did those of Rainy Lake in 1987 -- there are very few low growth or erect aquatics, and some thin-stem emergents appeared in a low water year. Along the c transect, Namakan Lake is depauperate in both low growth and erect aquatics; there is virtually no cover present in the upper portion of the water column. Mat formers and low rosettes are dominant, and these structure types present less surface area for colonization than the low growth aquatics of Lac La Croix. Along the d transect, Namakan Lake is more similar to Lac La Croix; however, the mat formers and low rosettes favored by drawdowns are also present.

Influence of Aquatic Vegetation on Aquatic Fauna

Physical and Biotic Interactions. Rooted aquatic macrophytes play a major role in the productivity and biogeochemical cycles of freshwater lakes because they provide a link between the sediments and the overlying water column. They are also intermediate between plankton and fish in the residence time of specific nutrients within aquatic systems (Carpenter and Lodge 1986). Macrophytes directly provide structural habitat for aquatic fauna, and they also affect other aspects of the physical environment in which the fauna live.

Carpenter and Lodge (1986) reviewed the effects of macrophytes on the physical environment and concluded that variations in macrophyte biomass could have major effects on aquatic ecosystems. Macrophytes provide a canopy that blocks light and thus affects the productivity of underlying macrophytes and epiphytes. Shading also reduces water temperatures and can create temperature gradients within the underlying water column. Water flow is retarded by macrophyte stands, and as a result, fine sediments that would otherwise be eroded are deposited. Biogeochemical processes are affected by macrophytes, including oxygenation of both water and sediment, mobilization of metals and phosphorus in the sediments, control of inorganic carbon speciation and pH, and uptake and release of organic carbon and nutrients during growth and decomposition.

Carpenter and Lodge (1986) also reviewed the biotic interactions of macrophytes and other plant and animal groups. Macrophytes are colonized by epiphytes, including microbes and algae. The epiphytes provide food for invertebrate grazers and also distract grazers from eating macrophytes. The invertebrates find food in macrophyte areas and also refuge from predation and sites for oviposition. Dead macrophytes and their associated bacteria are a food source for detritivores. Living macrophytes are a direct food source for aquatic organisms ranging from invertebrate grazers to waterfowl to fish to muskrats (Ondatra zibethicus). They also provide shelter for many of these organisms.

Clearly, macrophytes occupy an important position in aquatic ecosystems, but different macrophyte communities represent different habitats for aquatic fauna. Much of the difference depends on the species diversity, density, and structural aspects of the plants within the macrophyte community. Engel (1985) prepared a comprehensive account of the interactions of the aquatic community with submersed macrophytes in a Wisconsin lake. He concluded that a dynamic community of macrophytes that coupled structure with function had developed in the lake. Finely branched foliage maximized biomass and habitat structure, and the vegetation was vertically stratified into a three-dimensional, intricately structured macrophyte community. The macrophytes supported a wide range of algae and invertebrates, increased the diversity of zooplankton, and segregated fish by size. Dense plant beds were usually devoid of fish and provided refuge for invertebrates escaping fish predation. Less dense plant beds sheltered small fish but restricted larger ones. Openings in the canopy provided cruising lanes for largemouth bass foraging for smaller fish.

The relationships between macrophyte community structure and the various individual components of the faunal community are well-documented, although not for any single aquatic system. The effects of structural variation in macrophyte communities should be applicable to the regulated lakes of Voyageurs National Park. Previous sections of this report showed that different hydrologic regimes produced differences in macrophyte community composition (Table 1, Figure 3) and also in the morphological structure of the plant community (Table 2). The general structural groups of the 30 most important taxa along transects **b**, **c**, and **d** are depicted graphically in Figure 5 to provide a general view of the habitat as it might be viewed by aquatic fauna. Incorporating references from other individual studies and focusing on selected organisms present in Rainy and Namakan lakes, the possible effects of alteration of habitat resulting from hydrologic alteration will be explored.

Invertebrates. Kraft (1988) compared the benthic macro-invertebrates of Rainy Lake and three lakes in Namakan Reservoir at 1, 2, 3, 4, and 5 m depths to assess the effects of winter drawdown. In general, he observed that invertebrate species richness at the 1 and 2 m depths was greatest in Rainy Lake. At the 3, 4, and 5 m depths not affected by drawdown, species richness was greater in Namakan Reservoir. In Rainy Lake, diversity was greatest at 1 m and decreased with depth; in Namakan Reservoir, the greatest diversity occurred at 3 m or deeper. Kraft concluded that these differences were the result of excessive winter drawdowns in Namakan Reservoir and largely due to stranding of organisms. The differences in habitat provided by macrophytes at various depths may also be a factor, however.

Many invertebrate taxa are associated with aquatic macrophytes, and several theories concerning the associations have been espoused. Most authors agree that some invertebrates show definite

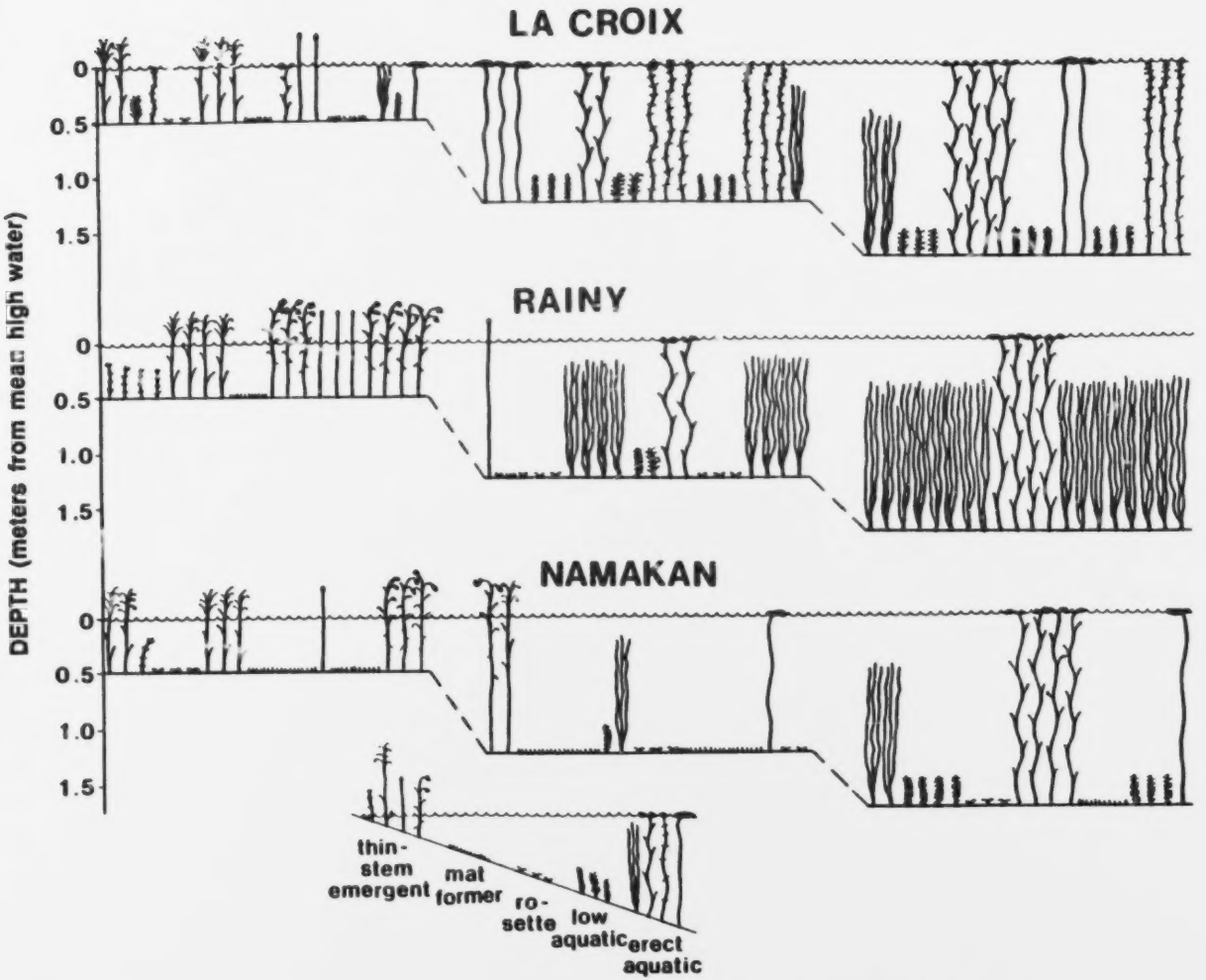

Figure 5. Diagrammatic cross-sections of the littoral zone of study sites in Lac La Croix, Rainy Lake, and Namakan Lake. The general structural groups of the 30 most important taxa, as might be viewed by aquatic fauna, are depicted at the water depths sampled along transects **b** (0.5 m), **c** (1.25 m), and **d** (1.75 m).

preferences for certain macrophyte taxa (Rosine 1955, Krull 1970, Gerrish and Bristow 1979, Dvorak and Best 1982, Cyr and Downing 1988a, 1988b) and that there are seasonal variations in invertebrate use of macrophytes (Rosine 1955, Rooke 1986, Brown et al. 1988). Murkin et al. (1982) concluded that areas with less shading from macrophyte litter would have greater substrate temperatures and, thus, greater invertebrate productivity.

Krecker (1939) hypothesized that plants with dissected leaves would support more invertebrates than those with broad leaves, presumably because they offer more colonizing surface. Others (Andrews and Hasler 1943, Gerking 1957, Gerrish and Bristow 1979) have confirmed this theory, but still others (Brown et al. 1988, Cyr and Downing 1988a) have collected contradictory data -- invertebrate abundance is not related to leaf dissection. Cyr and Downing (1988b) found that macrophyte beds with high areal plant biomass in lakes with high total phosphorus supported the greatest invertebrate abundance, and Voights (1976) found maximum invertebrate numbers when beds of submersed plants were interspersed with emergent vegetation.

The work of Brown et al. (1988) may have the best application to the relationships between invertebrates and the altered macrophyte communities of the regulated lakes of Voyageurs National Park. They found that both the species richness and density of invertebrates in Lake St. Clair increased as the taxonomic diversity of the macrophyte community increased. They concluded that invertebrate abundance and diversity were not related to surface area, per se. Instead, the vertically structured heterogeneity of surface area within the water column resulting from understory and overstory macrophytes created more habitat variety. The occurrence of both low-growth and upright (erect) growth forms produced the best habitat.

Translating the conclusions of Brown et al. (1988) to the lakes depicted in Figure 5, it seems that invertebrate habitat would be maximized along all transects of Lac La Croix. In Rainy Lake, transect **d** would be considered poor habitat because only erect macrophytes are present. In Namakan Lake, transect **c** would be poor habitat because there are few erect macrophytes extending through the water column. The remaining transects in Rainy and Namakan lakes have more vertical structural diversity, but they are less diverse than their counterparts in Lac La Croix and would not offer equivalent habitat. If natural water-level fluctuations were restored on Rainy and Namakan lakes and the plant communities responded accordingly, the amount of structurally diverse habitat for invertebrates should increase.

Three of the taxa specifically identified by Kraft (1988) as being affected by water-level regulation in Voyageurs National Park have affinities for aquatic vegetation. They may be responding to vegetation changes, as well as being physically stranded.

The nymph of the mayfly, Caenis, is often found among aquatic vegetation (McCafferty 1981); typical habitat is quiet water at the

edge of lakes overgrown with vegetation (Edmunds et al. 1976). The data of Kraft (1988) show that 80% of the nymphs collected in Rainy Lake were from the 1 m depth. In Namakan Reservoir, only 53% were from this depth that approximates the **c** transect (Figure 5); the remaining 47% were shifted to deeper waters where more erect and low growth aquatic plants occur.

The great majority of gastropods occur in shallow water (less than 3 m deep) because they are vegetarians and there is an abundance of food there. Some taxa, such as Physa, Gyraulus, and the Hydrobiidae, are found in greatest abundance where there is a moderate amount of aquatic vegetation (Voights 1976, Pennak 1978). In Rainy Lake, Kraft (1988) found that 82% of the gastropods collected were from the 1 m depth. Only 26% of the gastropods collected in Namakan Reservoir were from the 1 m depth where vegetation was sparse; 63% were collected at the 2 m depth that more closely approximates the **d** transect. This transect is in the winter drawdown zone, so drawdown and stranding may not be the cause for redistributing gastropod populations. Alterations in the structure of the plant community and the habitat that it provides may have caused the shift in density.

The isopod, Asellus, seldom comes into open water but remains hidden under rocks, vegetation, and debris; it is rarely found in water more than a meter deep (Pennak 1978). Voights (1976) found Asellus to be most common in the emergent zone of Iowa marshes where there was floating dead vegetation. In Rainy Lake, 99% of the Asellus collected were from the 1 m depth (Kraft 1988). None were collected in Namakan Reservoir, where winter drawdown extends far below the 1 m depth and the vegetation at 1 m is sparse. Again, vegetation changes may have affected the ability of this invertebrate to survive.

Muskrats. The greatest effect of water-level regulation on muskrats in Voyageurs National Park is the loss of access to lodges that were built during stable water periods in late summer or early autumn and then dewatered during the winter (Bellrose and Low 1943, Thurber and Peterson 1988). However, the type of food that muskrats have access to is affected also. When ice forms on Lac La Croix, water levels have already receded about one meter from the springtime high; they remain fairly stable during the winter. Despite the thickness of the ice, it is reasonable to assume that muskrats have access to the plants occurring along the **c** and **d** transects during most of the winter. Potential foods include Potamogeton, Nymphaea odorata, Myriophyllum exalbescens, and Vallisneria americana. These are not preferred muskrat foods, but muskrats seem to feed on what is available (Errington 1941, Stearns and Goodwin 1941, Takos 1947, Bellrose 1950).

In Rainy Lake, muskrat lodges would probably be built in water deep enough to provide access to **b** transect foods, such as Carex, Eleocharis, Glyceria borealis, and Polygonum lapathifolium, for part of the winter. Plants on the **c** and **d** transects, such as Potamogeton, Sagittaria, Myriophyllum exalbescens, Sparganium

fluctuans, and Vallisneria americana, would probably be accessible all winter; however, some foods available at Lac La Croix (Nymphaea odorata) do not grow at these depths in Rainy Lake.

In Namakan Lake where the problem of lodge dewatering is the greatest, the vegetation on even the c and d transects is not available for much of the winter. This does not leave much submersed food accessible under the ice. Over-winter survival of muskrats is believed to be very low in the Namakan Reservoir lakes (R. Peterson, pers. comm.); lack of food may be one cause for poor survival. If natural water-level fluctuations were restored, access to foods such as Potamogeton, Sagittaria, Nymphaea odorata, Myriophyllum exalbescens, and Vallisneria americana would be increased during the winter. In addition, more emergent vegetation used as food by muskrats would likely grow in the littoral zone if a water regime that included summertime drawdowns was restored. A greater interspersion of emergent and open aquatic habitat may also reduce the intensity of mink predation on muskrats (Proulx et al. 1987).

Avifauna. Reiser (1988) encountered 14 species of birds that utilized the portions of Rainy Lake and Namakan Reservoir affected by water-level fluctuations. Most of these species have affinities for wetland and aquatic vegetation; included are ring-necked grebe (Podiceps grisegena), pie-billed grebe (Podilymbus podiceps), American bittern (Botaurus lentiginosus), mallard (Anas platyrhinchos), blue-winged teal (Anas discors), Virginia rail (Rallus limicola), sora (Porzana carolina), yellow rail (Coturnicops noveboracensis), black tern (Chlidonias niger), long-billed marsh wren (Telmatodytes palustris), swamp sparrow (Melospiza georgiana), yellow-headed blackbird (Xanthocephalus xanthocephalus), and red-winged blackbird (Agelaius phoeniceus) (Johnsgard 1956, Weller and Spatcher 1965, Weller 1981, Reiser 1988). Reiser attributed decreased reproductive rates of some species to flooding of nests when water levels were increased in June of each year. However, she also recognized that depauperate nesting sites may have resulted from alterations in plant communities caused by water-level regulation.

It is well-understood that many species of birds are associated with wetland and aquatic macrophyte communities, and some display definite associations with particular vegetational stages. Johnsgard (1956) attributed these associations to the presence of suitable nest substrate, protective cover, food availability, territorial requirements, or combinations of these factors. He found that environmental changes caused by fluctuating water levels resulted in a redistribution of bird populations throughout a system of wetlands in east-central Washington that were affected by dam construction. Bird species remained a part of the biotic community only as long as the successional stage of the vegetation was within the tolerance limits of the species (Johnsgard 1956).

The vegetation stage commonly recognized as ideal for many bird species is the hemi-marsh, a 1:1 ratio of emergent vegetation and

open water (Weller and Spatcher 1965). However, Prince (1985) found fewer species nesting in areas with poorly developed submersed vegetation and concluded that the value of the submersed community is underrated. The physical structure of the vegetation, rather than its taxonomic composition, is of greatest importance to nesting birds (Weller 1978).

Only the near-shore areas of Lac La Croix, Rainy Lake, and Namakan Lake would provide the combination of emergent and submersed vegetation deemed ideal for nesting and cover (Figure 5). However, many of the emergents depicted in Figure 5, especially for Rainy Lake, were annuals that emerged as a result of unusually low water levels in 1987. Thus, if natural water-level fluctuations were restored, a gradual drawdown of water levels in Rainy and Namakan lakes during the summer might encourage the growth of emergent vegetation over a wider area in normal years.

As stated previously, food availability also determines the suitability of avian habitat. Aquatic vegetation (as foliage, shoots, tubers, and seeds) constitutes a portion of the diet of many birds (Weller 1981). However, invertebrates often represent a greater part of the diet. For instance, Murkin et al. (1982) concluded that although blue-winged teal and mallards preferred hemi-marsh habitat, their densities were dependent on invertebrate abundance. Thus, a loss of invertebrate numbers and diversity on transect **d** of Rainy Lake and transect **c** of Namakan Lake because structurally diverse vegetation was lacking could result in decreased food availability for some bird species.

Fish. Kallemeyn (1987a, 1987b) studied year class strength of northern pike (Esox lucius) and yellow perch (Perca flavescens) in Rainy Lake and Namakan Reservoir. These species have well-documented associations with aquatic macrophyte communities (Scott and Crossman 1973, Lee et al. 1980, Becker 1983). Kallemeyn found that the reproductive success of both species was greater in years with higher lake levels in the spring and concluded that the higher lake levels provided access to increased areas of flooded vegetation that could serve as spawning substrate. While this spawning activity is perhaps the most important interaction between fish, water levels, and vegetation at Voyageurs National Park, there are other fish species and other values, such as feeding and nursery habitat, that are worthy of further discussion.

Forty-eight species of fish have been found in the lakes of Voyageurs National Park (L. Kallemeyn, pers. comm.). Twelve of the species found in the regulated lakes are known to utilize wetland or aquatic macrophyte communities during one or more life history stages (Scott and Crossman 1973, Lee et al. 1980, Becker 1983, Dawson and Hellenthal 1986, Janacek 1988). These species are: muskellunge (Esox masquinongy), northern pike, golden shiner (Notemigonus crysoleucas), blacknose shiner (Notropis heterolepsis), black bullhead (Ictalurus melas), tadpole madtom (Noturus gyrinus), rock bass (Ambloplites rupestris), pumpkinseed (Lepomis gibbosus), bluegill (Lepomis macrochirus), largemouth bass

(Micropteris salmoides), black crappie (Pomoxis nigromaculatus), and yellow perch. The taxonomic diversity and structural complexity of the vegetation play major roles in determining the habitat values of the plant communities to these fish.

Poe et al. (1986) found that species richness and abundance of aquatic macrophytes had the most influence on the fish community structure in sites studied in Lake St. Clair. Crowder and Cooper (1979) hypothesized that the maximum feeding efficiency and growth of fish would occur at intermediate levels of structural complexity. In experimental pond studies, Crowder and Cooper (1982) noted that increased structural complexity reduced predator efficiency by reducing invertebrate prey capture rates. Dense structure inhibited foraging and allowed prey and predator to coexist. Sparse structure allowed for efficient foraging and resulted in an unstable system. They concluded that intermediate macrophyte density may be the best habitat both in terms of foraging and growth of the predator and stability of the fish-invertebrate prey interaction. As indicated in the previous section on invertebrates, prey diversity and the availability of specific preferred food organisms for foraging by fish may also be affected by differences in the structural complexity of the macrophyte community.

An important aspect of the piscivore fish-prey interaction is visibility. Savino and Stein (1982, 1989a) noted that increased structural complexity of simulated vegetation produced visual barriers and altered the behavior of both largemouth bass (predator) and bluegills (prey). Increased structural complexity did not deter northern pike from their ambushing attack strategy; however, it decreased their visual contact with prey and reduced their capture rate on bluegills (Savino 1985, Savino and Stein 1989a, 1989b). Helfman (1979) associated the attraction of fish to floats (as in leaves of water lilies) with visibility. A prey species in the shade of a floating object is less conspicuous to a predator in the sunlight and also has a better view of the predator. Conversely, a predator in the shade has a better view of passing prey.

Coastal wetland and macrophyte communities support high densities and diversities of young fish (Chubb and Liston 1986). Holland and Huston (1984) found that young-of-the-year northern pike avoided open water areas but used both emergent and submersed vegetation for cover and feeding, with a preference for submersed macrophyte beds. The structure and density of vegetation may produce physical barriers that restrict fish movement, thus providing nursery stocks with refuge from larger fish. Engel (1987, 1988) found that small bass and bluegills avoided bare areas and sought shelter among plant foliage, while submersed macrophytes at a density above 90 g/m^2 functioned as a screen to selectively exclude larger fish (predators). The small fish also had difficulty in penetrating plant beds denser than 300 g dry wt/m^2.

The suitability of vegetated areas for spawning is determined by timing in relation to water depth and temperature and by the physical nature of the vegetation. Northern pike prefer to spawn

on mats of grasses and sedges that remain from the previous growing season (Franklin and Smith 1963, McCarraher and Thomas 1972). However, if water levels are too low at the time that water temperatures reach 8 to 12° C and spawning begins (Inskip 1982), the preferred substrate may be out of water and unavailable. Yellow perch spawn at temperatures from 7 to 13° C and prefer to use areas of submersed vegetation (Krieger et al. 1983). Again, if water levels are too low when spawning temperatures are reached, the vegetation will not be available for use. These adverse conditions were characterized for Namakan Reservoir by Kallemeyn (1987a, 1987b). Others have also shown the relationship between successful spawning and water levels for northern pike (Johnson 1957, Franklin and Smith 1963, Hassler 1970) and yellow perch (Nelson and Walburg 1977, Martin et al. 1981), and similar cases might be made for other species present in Rainy and Namakan lakes.

We compared the spawning, nursery, and adult feeding habitat requirements (Scott and Crossman 1973, Lee et al. 1980, Becker 1983, Dawson and Hellenthal 1986, Janacek 1988) of the fish that are found in Voyageurs National Park to the habitat provided by the macrophytes along the **b**, **c**, and **d** transects of the study lakes (Figure 5), the water-level regimes (Figure 2) that determine accessibility of the macrophytes, and the temperature regimes (L. Kallemeyn, pers. comm.) that determine the initiation of spawning. This discussion is limited to the fish species that make major uses of macrophytes and are found in Rainy Lake, the five lakes that comprise Namakan Reservoir (L. Kallemeyn, pers. comm.), or Lac La Croix (Crossman 1976, D. Friedl, pers. comm.).

The plant communities along all transects in Lac La Croix are structurally diverse and of intermediate density. Plant materials suitable as spawning substrate are available to the applicable fish species at the proper depth (Table 3) when the water reaches critical temperatures. Similarly, suitable nursery and adult feeding habitats are available for all species. The habitat provided along the **b** transect differs somewhat from that in deeper water, but the **c** and **d** transects have similar habitat values.

The predicted fish use of the **b** and **c** transects in Rainy Lake does not differ from that in Lac La Croix, except that three additional species (muskellunge, black bullhead, largemouth bass) are present. The **d** transect does not differ from Lac La Croix in spawning or nursery habitat, but macrophyte cover extending throughout the water column could limit efficient use of this area for feeding by adult northern pike, yellow perch, and muskellunge.

The predicted fish use of transect **b** in Namakan Reservoir for nursery and adult feeding habitat and of transect **d** for all habitat purposes is the same as that in Lac La Croix, except that three additional species (black bullhead, bluegill, largemouth bass) are present. Unlike Lac La Croix, northern pike and yellow perch cannot use vegetation along the **b** transect in Namakan Reservoir for spawning because it has not yet been flooded when spawning occurs. Transect **a** (the shoreline) has thus far been omitted from this discussion because the vegetation does not differ much between

Table 3. Predicted fish use of macrophytes as spawning, nursery, and adult feeding habitat along transects b, c, and d in Lac La Croix, Rainy Lake, and Namakan Reservoir (refer to Figure 5).

LAKE	ACTIVITY	TRANSECT b 0.5 m	TRANSECT c 1.25 m	TRANSECT d 1.75 m
LAC LA CROIX	Spawning	northern pike black crappie yellow perch	golden shiner yellow perch	golden shiner yellow perch
	Nursery	northern pike rock bass pumpkinseed black crappie yellow perch	northern pike golden shiner rock bass pumpkinseed black crappie yellow perch	northern pike golden shiner rock bass pumpkinseed black crappie yellow perch
	Adult Feeding	golden shiner blacknose shiner rock bass	northern pike golden shiner blacknose shiner tadpole madtom rock bass pumpkinseed black crappie yellow perch	northern pike golden shiner blacknose shiner tadpole madtom rock bass pumpkinseed black crappie yellow perch
RAINY LAKE	Spawning	muskellunge[1,2] northern pike black bullhead[4] largemouth bass[4] black crappie yellow perch	golden shiner black bullhead[4] largemouth bass[4] yellow perch	golden shiner yellow perch
	Nursery	northern pike black bullhead[4] rock bass pumpkinseed largemouth bass[4] black crappie yellow perch	muskellunge[1,2] northern pike golden shiner black bullhead[4] rock bass pumpkinseed largemouth bass[4] black crappie yellow perch	muskellunge[1,2] northern pike golden shiner rock bass pumpkinseed largemouth bass[4] black crappie yellow perch
	Adult Feeding	golden shiner blacknose shiner black bullhead[4] rock bass	muskellunge[1,2] northern pike golden shiner blacknose shiner black bullhead[4] tadpole madtom rock bass pumpkinseed largemouth bass[4] black crappie yellow perch	golden shiner blacknose shiner tadpole madtom rock bass pumpkinseed black crappie
NAMAKAN RESERVOIR	Spawning	black bullhead[1,3] black crappie	golden shiner largemouth bass[1,4] black crappie	golden shiner largemouth bass[1,4] yellow perch
	Nursery	northern pike black bullhead[1,3] rock bass pumpkinseed bluegill[1,4,5] largemouth bass[1,4] black crappie yellow perch		northern pike golden shiner black bullhead[1,3] rock bass pumpkinseed bluegill[1,4,5] largemouth bass[1,4] black crappie yellow perch
	Adult Feeding	golden shiner blacknose shiner black bullhead[1,3] rock bass	golden shiner blacknose shiner rock bass pumpkinseed bluegill[1,4,5] largemouth bass[1,4] black crappie yellow perch	northern pike golden shiner blacknose shiner black bullhead[1,3] tadpole madtom rock bass pumpkinseed bluegill[1,4,5] largemouth bass[1,4] black crappie yellow perch

[1]does not occur in Lac La Croix
[2]does not occur in Namakan Reservoir
[3]occurs only in Kabetogama Lake of Namakan Reservoir
[4]occurs only in Sand Point Lake of Namakan Reservoir
[5]does not occur in Rainy Lake

lakes. Although this transect is often out of the water and provides only limited aquatic habitat, it can offer suitable spawning habitat for northern pike and yellow perch in Lac La Croix during high water years. In Namakan Reservoir, the **a** transect would only be accessible for spawning in extremely high water years because the water levels are regulated to peak at a later date.

Muskellunge were once stocked in Kabetogama Lake of Namakan Reservoir, but they failed to become established there (D. Friedl, pers. comm.). There are many possible causes for the failure of this stocking effort, but the lack of access to nearshore vegetation for spawning because of low springtime water levels is one probable cause. Low water levels in the spring also prevent yellow perch from spawning on vegetation on the **c** transect in Namakan Reservoir. The sparse nature of the vegetation on the **c** transect precludes its use as nursery habitat by any species because protective cover is lacking. Adult tadpole madtoms would avoid this area for feeding because cover is lacking, and adult northern pike would not be successful in ambushing prey there because they would be highly visible.

Regulation of water levels on Rainy Lake and Namakan Reservoir does affect fish habitat. However, the adverse effects in Rainy Lake are in deeper waters (transect **d**) and can be compensated for by habitat available in shallower water (transect **c**). Those species that require the use of wetland or aquatic macrophyte communities during one or more life history stages can find suitable habitat. In Namakan Reservoir, conditions are more limiting. The **d** transect does provide some structurally diverse habitat to compensate for the poor habitat present along the **c** transect. However, those fish species that spawn in nearshore vegetated areas in the spring are severely limited by the current regulation scheme that delays water-level peaks and does not allow access to the vegetation during the spawning season.

CONCLUSIONS

This study was conducted for the purpose of determining the effects of water-level regulation in Rainy and Namakan lakes on (1) community composition of aquatic macrophytes, (2) specific macrophyte taxa, and (3) aquatic fauna habitat, as related to macrophyte alterations. Effects were shown in all cases.

The aquatic macrophyte communities of Lac La Croix, Rainy Lake, and Namakan Lake differed at all depths, and the differences were more pronounced along the deeper transects, as shown by the DCA ordination. The differences in plant communities can be attributed to water-level regulation because the sampling was designed to focus on depths with different ecological attributes related to water regimes. The communities in Lac La Croix resembled those expected at depths that experienced permanent inundation or springtime flooding combined with summer or winter drawdown. Altered hydrology in Rainy and Namakan lakes not only resulted in a difference in species that dominated each transect, it created

differences in the structural nature of the vegetation. The d transect of Rainy Lake is never disturbed by dewatering, and the stable environment allows a few erect aquatics to dominate, resulting in a lack of both taxonomic and structural diversity. The c transect of Namakan Lake is annually exposed to the disturbance effects of desiccation and ice action. Mat formers and low rosettes are favored by these conditions, again resulting in a lack of structural diversity.

The three lakes in this study generally contained the same plant species; it was the abundance of individual species at each depth that differed. However, several dominant taxa in Lac La Croix were rare or absent in the regulated lakes. These taxa included: Thelypteris palustris in both Rainy and Namakan lakes, Glyceria borealis, Nymphaea odorata, and Chara in Rainy Lake, and Bidens beckii and Zizania palustris in Namakan Lake. Competitive exclusion or intolerable environmental conditions (e.g., flooding, desiccation, freezing) could be responsible for the loss of these taxa and the increased dominance of others in the regulated lakes. Polygonum lapathifolium was not found in Lac La Croix but was prominent in both Rainy and Namakan lakes. Eleocharis acicularis, Ranunculus reptans, Tillaea aquatica, and Isoetes echinospora all were of increased importance in Namakan Lake.

Alterations of aquatic plant communities in Rainy and Namakan lakes have resulted in altered habitat values for various faunal organisms, both through changes in the structural complexity of the plant beds and through lost availability of preferred plant species. Muskrats probably lack adequate food supplies under the ice following winter drawdown in Namakan Lake. Invertebrates could be affected by the loss of structural complexity along the d transect of Rainy Lake and the c transect of Namakan Lake. Gastropods, the mayfly Caenis, and the isopod Asellus in Namakan Lake seem most affected. Birds have less hemi-marsh habitat available in the regulated lakes, and decreased invertebrate populations translate to a decreased food supply for many of them. Macrophytes extending throughout the water column along the d transect in Rainy Lake could limit use of that area for adult feeding by northern pike, yellow perch, and muskellunge. Greater fish habitat problems occur on Namakan Lake where northern pike and yellow perch do not have access to plant beds for spawning because of low water levels in the spring. Fish use of the c transect for nursery and adult-feeding habitat is also limited because virtually no protective cover is available in the water column.

The integrity and viability of these lake systems increases with increased diversity, and the amount of disturbance determines diversity. In his "intermediate disturbance hypothesis," Connell (1978) proposed that the highest diversity is maintained at intermediate scales of disturbance. Keddy (1983) confirmed this hypothesis as applied to shoreline vegetation in his study of an Ontario lake. The water levels in Lac La Croix vary naturally from year to year, with occasional annual fluctuations as small as 0.3.m and as great as 3.0 m (1926-1987 water-level records). This variability spreads the effects of extreme environmental conditions

out across a wider area over time (e.g., the location of ice damage changes from year-to-year because the water level at freeze-over changes). Thus, there is a longer time interval between similar disturbances at any specific depth, and more species can invade to increase local diversity (Connell 1978).

The hydrologic regime at Lac La Croix represents intermediate disturbance. There is too little disturbance from water-level fluctuations in Rainy Lake, and a stable macrophyte community with little diversity has developed at depths that never undergo drawdown. There is too much disturbance from water-level fluctuations in Namakan Lake; only those species that are very well adapted to the pervasive physical disruptions or that can invade and mature quickly have survived at depths that undergo long winter drawdowns. Both Rainy and Namakan lakes could benefit from a return to more natural hydrologic regimes. Namakan Reservoir should be regulated to reach its maximum water level at the beginning of June. Summer drawdowns should occur at both Rainy Lake and Namakan Reservoir so that near-minimums are reached before ice forms. Finally, the amplitude of the drawdown should be increased at Rainy Lake and decreased at Namakan Reservoir to approximate natural drawdowns of 1.8 - 1.9 m, and there should be variability between years. As shown for Lac La Croix, these hydrologic conditions should, over time, result in more diverse macrophyte communities throughout the littoral zone of the regulated lakes and more diverse habitats for aquatic fauna.

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Appendix. Latin names and common names of plant taxa encountered in study of Lac La Croix, Rainy Lake, and Namakan Lake.

Latin Name	Common Name
Acer rubrum	Red Maple
Acorus calamus	Sweet-flag
Agrostis hyemalis	Ticklegrass
Alnus spp.	Alder
Anemone canadensis	Canada Anemone
Aster spp.	Aster
Betula spp.	Birch
Bidens beckii	Water Marigold
Bidens cernua	Nodding Bur Marigold
Calamagrostis canadensis	Blue-joint Grass
Campanula aparinoides	Marsh Bellflower
Cardamine pensylvanica	Pennsylvania Bitter Cress
Carex crawfordii	Crawford's Sedge
Carex hirta	Hairy Sedge
Carex lacustris	Lake-bank Sedge
Carex rostrata	Beaked Sedge
Carex stricta	Tussock Sedge
Carex sychnocephala	Dense Long-beaked Sedge
Carex vesicaria	Inflated Sedge
Carex viridula	Green Sedge
Chara spp.	Muskgrass
Cicuta bulbifera	Bulblet-bearing Water Hemlock
Cirsium sp.	Thistle
Cyperus aristatus	Umbrella Sedge
Cyperus strigosus	Nut Grass
Elatine minima	Waterwort
Eleocharis acicularis	Needle Spike-rush
Eleocharis obtusa	Blunt Spike-rush
Eleocharis smallii	Small's Spike-rush
Epilobium coloratum	Cinnamon Willow-herb
Equisetum arvense	Horsetail
Equisetum fluviatile	Pipes
Fimbristylis autumnalis	Autumn Sedge
Fragaria virginiana	Wild Strawberry
Fraxinus spp.	Ash
Galium trifidum	Small Bedstraw
Geranium bicknellii	Northern Cranesbill
Gerardia tenuifolia	Slender False Foxglove
Glyceria borealis	Northern Manna Grass
Glyceria canadensis	Rattlesnake Grass
Glyceria grandis	Reed Manna Grass
Hemicarpha micrantha	Common Hemicarpha
Hypericum majus	Larger Can. St. John's-wort
Impatiens capensis	Spotted Touch-me-not
Isoetes echinospora	Quillwort
Juncus brevicaudatus	Narrow-pannicled Rush
Juncus effusus	Common Rush
Juncus pelocarpus	Brown-fruited Rush
Lathyrus palustris	Marsh Pea
Lemna spp.	Duckweed
Littorella uniflora	Plantain Shore-weed
Lycopus americanus	Common Water Horehound

Appendix (continued)

Lysimachia terrestris	Swamp Candles
Lysimachia thyrsiflora	Tufted Loosestrife
Mentha arvensis	Wild Mint
Myrica gale	Sweet Gale
Myriophyllum spp.	Water-milfoil
Najas flexilis	Slender Naiad
Nitella sp.	Nitella
Nuphar variegata	Bullhead Lily
Nymphaea odorata	White Water Lily
Onoclea sensibilis	Sensitive Fern
Oxalis fontana	Wood-sorrel
Panicum sp.	Panic Grass
Poa pratensis	Kentucky Bluegrass
Polygonum amphibium	Water Smartweed
Polygonum lapathifolium	Nodding Smartweed
Polygonum punctatum	Dotted Smartweed
Polygonum sagittatum	Arrow-leaved Tear-thumb
Populus spp.	Poplar
Potamogeton amplifolius	Large-leaved Pondweed
Potamogeton epihydrus	Ribbon-leaved Pondweed
Potamogeton foliosus	Leafy Pondweed
Potamogeton gramineus	Grass-leaved Pondweed
Potamogeton richardsonii	Richardson's Pondweed
Potamogeton robbinsii	Fern Pondweed
Potamogeton spirillus	Spiral Pondweed
Potamogeton vaseyi	Vasey's Pondweed
Potamogeton zosteriformis	Flat-stemmed Pondweed
Potentilla norvegica	Rough Cinquefoil
Potentilla palustris	Marsh Cinquefoil
Ranunculus longirostris	Whitewater Crowfoot
Ranunculus pennsylvanica	Bristly Crowfoot
Ranunculus reptans	Creeping Spearwort
Rorippa palustris	Yellow Cress
Rosa palustris	Swamp Rose
Sagittaria latifolia	Common Arrowhead
Sagittaria rigida	Stiff Arrowhead
Sagittaria spp.	Arrowhead
Scirpus cyperinus	Wool-grass
Scutellaria galericulata	Marsh Scullcap
Sium suave	Water Parsnip
Solidago graminifolia	Grass-leaved Goldenrod
Sparganium chlorocarpum	Green-fruited Bur-reed
Sparganium eurycarpum	Broad-fruited Bur-reed
Sparganium fluctuans	Floating Bur-reed
Spiraea alba	Meadowsweet
Stachys palustris	Woundwort
Subularia aquatica	Awlwort
Thelypteris palustris	Marsh Shield Fern
Tillaea aquatica	Pigmy-weed
Triadenum fraseri	Marsh St. John's Wort
Typha latifolia	Common Cattail
Utricularia vulgaris	Great Bladderwort
Vallisneria americana	Wild Celery
Verbena hastata	Blue Vervain
Veronica anagallis-aquatica	Water Speedwell
Viola spp.	Violet
Zizania palustris	Northern Wild Rice

The National Park Service's Midwest Region covers 33 park units located in 10 states in the Great Plains and Great Lakes area (Nebraska, Kansas, Missouri, Iowa, Minnesota, Wisconsin, Michigan, Illinois, Indiana, and Ohio). The physical and biological diversity of the Region is reflected in the variety of research conducted in the parks. Current research subjects range from a survey of prairie vegetation in several small parks to the ecology of boreal forests at Voyageurs; from threatened plants in a number of parks to endangered wolves at Isle Royale; from hydrology of springs at Ozark to air pollution at Indiana Dunes; and from recreational boating use patterns on the Lower Saint Croix to hiking and campground use at Isle Royale. For more information on the National Park Service's Midwest Regional science program, please write:

Regional Chief Scientist
National Park Service
Midwest Regional Office
1709 Jackson Street
Omaha, Nebraska 68102

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environment and cultural value of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

U.S. DEPARTMENT OF THE INTERIOR

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